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Title: Moving in the Anthropocene: Global reductions in terrestrial mammalian movements

Authors: Marlee A. Tucker,^{1,2*} Katrin Böhning-Gaese,^{1,2} William F. Fagan,^{3,4} John Fryxell,⁵ Bram Van Moorter,⁶ Susan C. Alberts,⁷ Abdullahi H. Ali,⁸ Andrew M. Allen,^{9,10} Nina Attias,¹¹ Tal Avgar,¹² Hattie Bartlam-Brooks,¹³ Buuveibaatar Bayarbaatar,¹⁴ Jerrold L. Belant,¹⁵ Alessandra Bertassoni,¹⁶ Dean Beyer,¹⁷ Laura Bidner,¹⁸ Floris M. van Beest,¹⁹ Stephen Blake,^{20,21} Niels Blaum,²² Chloe Bracis,^{1,2} Danielle Brown,²³ PJ Nico de Bruyn,²⁴ Francesca Cagnacci,^{25,26} Justin M. Calabrese,^{27,3} Constança Camilo-Alves,^{28,29} Simon Chamailé-Jammes,³⁰ Andre Chiaradia,^{31,32} Sarah C. Davidson,^{33,20} Todd Dennis,³⁴ Stephen DeStefano,³⁵ Duane Diefenbach,³⁶ Iain Douglas-Hamilton,^{37,38} Julian Fennessy,³⁹ Claudia Fichtel,⁴⁰ Wolfgang Fiedler,²⁰ Christina Fischer,⁴¹ Ilya Fischhoff,⁴² Christen H. Fleming,^{27,3} Adam Ford,⁴³ Susanne Fritz,^{1,2} Benedikt Gehr,⁴⁴ Jacob R. Goheen,⁴⁵ Eliezer Gurarie,^{3,46} Mark Hebblewhite,⁴⁷ Marco Heurich,^{48,49} A. J. Mark Hewison,⁵⁰ Christian Hof,¹ Edward Hurme,³ Lynne A. Isbell,^{18,51} René Janssen,⁵² Florian Jeltsch,²² Petra Kaczensky,^{6,53} Adam Kane,⁵⁴ Peter Kappeler,⁴⁰ Matthew Kauffman,⁵⁵ Roland Kays,^{56,57} Duncan Kimuyu,⁵⁸ Flavia Koch,^{40,59} Bart Kranstauber,⁴⁴ Scott LaPoint,^{20,60} Peter Leimgruber,²⁷ John D. C. Linnell,⁶ Pascual López-López,⁶¹ A. Catherine Markham,⁶² Jenny Mattisson,⁶ Emilia Patricia Medici,^{63,64} Ugo Mellone,⁶⁵ Evelyn Merrill,¹² Guilherme de Miranda Mourão,⁶⁶ Ronaldo G. Morato,⁶⁷ Nicolas Morellet,⁵⁰ Thomas Morrison,⁶⁸ Samuel L. Díaz-Muñoz,^{69,70} Atle Mysterud,⁷¹ Dejid Nandintsetseg,^{1,2} Ran Nathan,⁷² Aidin Niamir,¹ John Odden,⁷³ Robert B. O'Hara,^{1,74} Luiz Gustavo R. Oliveira-Santos,⁷⁵ Kirk A. Olson,¹⁴ Bruce D. Patterson,⁷⁶ Rogerio Cunha de Paula,⁶⁷ Luca Pedrotti,⁷⁷ Björn Reineking,^{78,79} Martin Rimmler,⁸⁰ Tracey L. Rogers,⁸¹ Christer Moe Rolandsen,⁶ Christopher S. Rosenberry,⁸² Daniel I. Rubenstein,⁸³ Kamran Safi,^{20,84} Sonia Saïd,⁸⁵ Nir Sapir,⁸⁶ Hall Sawyer,⁸⁷ Niels Martin Schmidt,^{19,88} Nuria Selva,⁸⁹ Agnieszka Sergiel,⁸⁹ Enkhtuvshin Shiilegdamba,¹⁴ João Paulo Silva,^{90,91,92} Navinder Singh,⁹ Erling J. Solberg,⁶ Orr Spiegel,⁹³ Olav Strand,⁶ Siva Sundaresan,⁹⁴ Wiebke Ullmann,²² Ulrich Voigt,⁹⁵ Jake Wall,³⁷ David Wattles,³⁵ Martin Wikelski,^{20,84} Christopher C. Wilmers,⁹⁶ John W. Wilson,⁹⁷ George Wittemyer,^{98,37} Filip Zięba,⁹⁹ Tomasz Zwijacz-Kozica,⁹⁹ Thomas Mueller^{1,2,27*}

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27
28
29

Affiliations:

¹Senckenberg Biodiversity and Climate Research Centre, Senckenberg Gesellschaft für Naturforschung, Senckenberganlage 25, 60325 Frankfurt (Main), Germany.

²Department of Biological Sciences, Goethe University, Max-von-Laue-Straße 9, 60438, Frankfurt (Main), Germany.

³Department of Biology, University of Maryland, College Park, MD, 20742, USA.

⁴SESYNC, University of Maryland, Annapolis, MD 21401, USA.

⁵Department of Integrative Biology, University of Guelph, 50 Stone Road, Guelph, Ontario, Canada, N1G 2W1.

⁶Norwegian Institute for Nature Research, PO Box 5685 Sluppen, NO-7485 Trondheim, Norway.

⁷Departments of Biology and Evolutionary Anthropology, Duke University, Durham NC 27708, USA.

⁸Hirola Conservation Programme, Garissa, Kenya.

⁹Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, 90183, Sweden.

¹⁰Radboud University, Institute for Water and Wetland Research, Department of Animal Ecology and Physiology, 6500GL, Nijmegen, The Netherlands.

¹¹Ecology and Conservation Graduate Program, Federal University of Mato Grosso do Sul, Campo Grande-MS, Brazil. Centro de Ciências Biológicas e da Saúde - Cidade Universitária s/n - Caixa Postal 549, Campo Grande, MS, 79070-900, Brazil.

¹²Department of Biological Sciences, University of Alberta, 1145 Saskatchwan Dr, Edmonton, Alberta Canada.

¹³Structure and Motion Laboratory, Royal Veterinary College, University of London, England.

¹⁴Wildlife Conservation Society, Mongolia Program, Ulaanbaatar, Mongolia.

¹⁵Carnivore Ecology Laboratory, Forest and Wildlife Research Center, Mississippi State University, Box 9690, Mississippi State, Mississippi, USA.

¹⁶Animal Biology Post-graduate Program, São Paulo State University, São José do Rio Preto, SP, 15054-000, Brazil.

¹⁷Michigan Department of Natural Resources, 1990 U.S. 41 South, Marquette, MI 49855, USA.

¹⁸Department of Anthropology and Animal Behavior Graduate Group, One Shields Ave., University of California, Davis, California, 95616, USA.

¹⁹Department of Bioscience, Aarhus University, Frederiksborgvej 399, 4000 Roskilde, Denmark.

²⁰Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Am Obstberg 1 D-78315 Radolfzell, Germany.

²¹Wildlife Conservation Society, 2300 Southern Boulevard, Bronx, New York, 10460, USA.

²²University of Potsdam, Plant Ecology and Nature Conservation, Am Mühlenberg 3, 14476 Potsdam, Germany.

²³Department of Biology, Middle Tennessee State University, PO Box 60, Murfreesboro, TN 37132, USA.

²⁴Mammal Research Institute, Department of Zoology & Entomology, University of Pretoria, Private Bag X20, Hatfield 0028, Gauteng, South Africa.

²⁵Department of Biodiversity and Molecular Ecology, Research and Innovation Centre, Fondazione Edmund Mach, via Mach 1, 38100 Italy.

²⁶Organismic and Evolutionary Biology Dept., Harvard University, 26 Oxford st 02138 Cambridge, MA, USA.

²⁷Smithsonian Conservation Biology Institute, National Zoological Park, Front Royal, VA, USA.

²⁸Évora University, Dep.Fitotecnia, Pólo da Mitra, Ap. 94, 7002-554 Évora, Portugal

²⁹ICAAM-Institute of Mediterranean Agricultural and Environmental Sciences, University of Évora, Évora, Portugal.

³⁰Centre d'Ecologie Fonctionnelle et Evolutive UMR 5175, CNRS - Université de Montpellier - Université Paul-Valéry Montpellier - EPHE, 1919 route de Mende, 34293 Montpellier Cedex 5, France.

³¹Phillip Island Nature Parks, Victoria, Australia

- 83 ³²School of Biological Sciences, Monash University, Australia
- 84 ³³Department of Civil, Environmental and Geodetic Engineering, The Ohio State University, 475
85 Hitchcock Hall, 2070 Neil Avenue, Columbus, OH 43210, USA.
- 86 ³⁴School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland Mail
87 Centre, New Zealand.
- 88 ³⁵Massachusetts Cooperative Fish and Wildlife Research Unit, University of Massachusetts,
89 Amherst, MA 01003, USA.
- 90 ³⁶U.S. Geological Survey, Pennsylvania Cooperative Fish and Wildlife Research Unit,
91 Pennsylvania State University, University Park, PA 16802, USA.
- 92 ³⁷Save the Elephants, P.O. Box 54667, Nairobi, Kenya, 00200.
- 93 ³⁸University of Oxford, Department of Zoology, OX1 3PS, UK.
- 94 ³⁹Giraffe Conservation Foundation, PO Box 86099, Eros, Namibia.
- 95 ⁴⁰German Primate Center, Behavioral Ecology & Sociobiology Unit, Kellnerweg 4, 37077
96 Göttingen, Germany.
- 97 ⁴¹Restoration Ecology, Department of Ecology and Ecosystem Management, Technische
98 Universität München, Emil-Ramann-Str. 6, 85354 Freising, Germany.
- 99 ⁴²Cary Institute of Ecosystem Studies, 2801 Sharon Turnpike, Millbrook NY 12545, USA.
- 100 ⁴³The Irving K. Barber School of Arts and Sciences, Unit 2: Biology, The University of British
101 Columbia, Okanagan campus, SCI 109, 1177 Research Road, Kelowna, BC Canada V1V 1V7.
- 102 ⁴⁴Department of Evolutionary Biology and Environmental Studies, University of Zurich,
103 Winterthurerstrasse 190, 8057 Zurich, Switzerland.
- 104 ⁴⁵Department of Zoology and Physiology, University of Wyoming, Laramie, WY 82071, USA.
- 105 ⁴⁶School of Environmental and Forest Sciences, University of Washington, Seattle, WA 98195,
106 USA.
- 107 ⁴⁷Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, College of
108 Forestry and Conservation, University of Montana, Missoula, MT 59812, USA.

- 109 ⁴⁸Bavarian Forest National Park, Department of Conservation and Research, Freyunger Straße 2,
110 94481 Grafenau, Germany.
- 111 ⁴⁹Chair of Wildlife Ecology and Management, Albert Ludwigs University of Freiburg,
112 Tennenbacher Straße 4, 79106 Freiburg, Germany.
- 113 ⁵⁰CEFS, Université de Toulouse, INRA, Castanet Tolosan, France.
- 114 ⁵¹Animal Behavior Graduate Group, One Shields Ave., University of California, Davis,
115 California, 95616, USA.
- 116 ⁵²Bionet Natuuronderzoek, Valderstraat 39, 6171EL Stein, The Netherlands.
- 117 ⁵³Research Institute of Wildlife Ecology, University of Veterinary Medicine, Vienna,
118 Savoyenstrasse 1, A-1160 Vienna, Austria.
- 119 ⁵⁴School of Biological, Earth and Environmental Sciences, University College Cork, Cork,
120 Ireland.
- 121 ⁵⁵U.S. Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Department
122 of Zoology and Physiology, University of Wyoming, Laramie, WY, USA.
- 123 ⁵⁶North Carolina Museum of Natural Sciences, 11 West Jones St., Raleigh NC 27601, USA.
- 124 ⁵⁷Department Forestry and Environmental Resources, North Carolina State University, Raleigh,
125 NC 27695, USA.
- 126 ⁵⁸Department of Natural Resource Management, Karatina university, P.O Box 1957- 10101,
127 Karatina, Kenya.
- 128 ⁵⁹Department of Psychology, University of Lethbridge, Lethbridge, Alberta T1K3M4, Canada.
- 129 ⁶⁰Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA.
- 130 ⁶¹University of Valencia, Cavanilles Institute of Biodiversity and Evolutionary Biology,
131 Terrestrial Vertebrates Group, C/ Catedrático José Beltrán 2, E-46980 Paterna, Valencia, Spain.
- 132 ⁶²Department of Anthropology, Stony Brook University, Stony Brook, NY 11794 USA.
- 133 ⁶³Lowland Tapir Conservation Initiative (LTCI), IPE - Instituto de Pesquisas Ecologicas &
134 IUCN/SSC Tapir Specialist Group (TSG).
- 135 ⁶⁴Rua Licuala, 622, Damha 1, CEP: 79046-150, Campo Grande, Mato Grosso do Sul, Brazil.

- 136 ⁶⁵Vertebrates Zoology Research Group, Departamento de Ciencias Ambientales y Recursos
137 Naturales, University of Alicante, Alicante, Spain.
- 138 ⁶⁶Embrapa Pantanal, Corumbá, MS, 79320-900, Brazil.
- 139 ⁶⁷National Research Center for Carnivores Conservation, Chico Mendes Institute for the
140 Conservation of Biodiversity. Estrada Municipal Hisaichi Takebayashi 8600 Atibaia-SP 12952-
141 011, Brazil.
- 142 ⁶⁸Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow,
143 UK.
- 144 ⁶⁹Center for Genomics and Systems Biology, Department of Biology, New York University, 12
145 Waverly Place New York, NY 10003, USA.
- 146 ⁷⁰Department of Microbiology and Molecular Genetics, University of California, Davis, One
147 Shields Avenue, Davis, CA 95616, USA.
- 148 ⁷¹Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of
149 Oslo, P.O. Box 1066 Blindern, NO-0316 Oslo, Norway.
- 150 ⁷²Movement Ecology Laboratory, Department of Ecology, Evolution and Behavior, Alexander
151 Silberman Institute of Life Sciences, The Hebrew University of Jerusalem, Edmond J. Safra
152 Campus, Jerusalem 91904, Israel.
- 153 ⁷³Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway.
- 154 ⁷⁴Department of Mathematical Sciences & Centre for Biodiversity Dynamics, NTNU, 7491
155 Trondheim, Norway.
- 156 ⁷⁵Department of Ecology, Federal University of Mato Grosso do Sul, Campo Grande, MS,
157 79070-900, Brazil.
- 158 ⁷⁶Integrative Research Center, Field Museum of Natural History, Chicago IL 60605, USA.
- 159 ⁷⁷Consorzio Parco Nazionale dello Stelvio, Bormio (Sondrio), Italy.
- 160 ⁷⁸Irstea, UR EMGR, Université Grenoble Alpes, 2 rue de la Papeterie, BP 76, 38402 St-Martin-
161 d'Hères, France.
- 162 ⁷⁹Biogeographical Modelling, Bayreuth Center of Ecology and Environmental Research
163 BayCEER, University of Bayreuth, Universitätsstr. 30, 95440 Bayreuth, Germany.

- 164 ⁸⁰Nationalpark Schwarzwald, Schwarzwaldhochstraße 2, 77889 Seebach, Germany.
- 165 ⁸¹Evolution and Ecology Research Centre, and School of Biological, Earth and Environmental
166 Sciences, University of New South Wales, Sydney, NSW, 2052, Australia.
- 167 ⁸²Pennsylvania Game Commission, 2001 Elmerton Avenue, Harrisburg PA 17110, USA.
- 168 ⁸³Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544,
169 USA.
- 170 ⁸⁴Department of Biology, University of Konstanz, 78467 Konstanz, Germany.
- 171 ⁸⁵Office National de la Chasse et de la Faune Sauvage, DRE-UCS-"Montfort"-01330 Birieux,
172 France.
- 173 ⁸⁶Department of Evolutionary and Environmental Biology, University of Haifa, 3498838 Haifa,
174 Israel.
- 175 ⁸⁷Western Ecosystems Technology, Inc., Laramie, WY 82070, USA.
- 176 ⁸⁸Arctic Research Centre, Aarhus University, 8000 Aarhus C, Denmark.
- 177 ⁸⁹Institute of Nature Conservation Polish Academy of Sciences, Mickiewicza 33, 31-120
178 Krakow, Poland.
- 179 ⁹⁰REN Biodiversity Chair, CIBIO/InBIO Associate Laboratory, Universidade do Porto, Campus
180 Agrário de Vairão, 4485-661 Vairão, Portugal.
- 181 ⁹¹Centre for Applied Ecology "Prof. Baeta Neves"/InBIO Associate Laboratory, Instituto
182 Superior de Agronomia, Universidade de Lisboa, Tapada da Ajuda, 1349-017 Lisbon, Portugal..
- 183 ⁹²Centre for Ecology, Evolution and Environmental Changes; Faculdade de Ciências da
184 Universidade de Lisboa, Campo Grande, 1749-016 Lisbon, Portugal.
- 185 ⁹³Department of Environmental Science and Policy, University of California, Davis, USA.
- 186 ⁹⁴Jackson Hole Conservation Alliance, 685 S Cache St, Jackson WY 83001, USA.
- 187 ⁹⁵Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine
188 Hannover - Foundation, Bischofsholer Damm 15, 30173 Hannover, Germany.
- 189 ⁹⁶Center for Integrated Spatial Research, Environmental Studies Department, University of
190 California, Santa Cruz, 1156 High St, Santa Cruz CA, 95060 USA.

191 ⁹⁷Department of Zoology and Entomology, University of Pretoria, Hatfield 0028, South Africa.

192 ⁹⁸1474 Campus Delivery, Dept Fish, Wildlife and Conservation Biology, Colorado State
193 University, Fort Collins, CO 80523 USA.

194 ⁹⁹Tatra National Park, Kuźnice 1, 34-500 Zakopane, Poland.

195 *Corresponding author: tucker.marlee@gmail.com; thomas.mueller@senckenberg.de

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Animal movement is fundamental for ecosystem functioning and species survival, yet the effects of the anthropogenic footprint on animal movements have not been estimated across species. Using a unique GPS-tracking database of 803 individuals across 57 species, we found that mammalian movements in areas with a comparatively high human footprint were on average two-to-three times smaller than those in areas with a low human footprint. We attribute this reduction to both behavioral changes of individual animals and the exclusion of species with long-range movements from areas with higher human impact. Global loss of vagility alters a key ecological trait of animals that not only affects population persistence, but also ecosystem processes, such as predator-prey interactions, nutrient cycling, and disease transmission.

With approximately 50-70% of the Earth's land surface currently modified for human activities (1), patterns of biodiversity and ecosystem functions worldwide are changing (2). The expanding footprint of human activities is not only causing the loss of habitat and biodiversity, but also affects how animals move through fragmented and disturbed habitats. The extent to which animal movements are affected by anthropogenic changes in the structure and composition of landscapes and resource changes has only been explored in local geographic regions or within single species. Such studies typically report decreasing animal movements, for example due to habitat fragmentation, barrier effects or resource changes (3–6), with only a few studies reporting longer movements as a result of habitat loss or altered migration routes (7, 8). Here we conducted a global comparative study examining how the human footprint affects movements of terrestrial non-volant mammals using Global Positioning System (GPS) location data of 803 individuals from 57 mammal species (Fig. 1 and Table S2). Mean species' mass ranged from 0.49 to 3940 kg and included herbivores, carnivores, and omnivores ($n = 28, 11, \text{ and } 18$ species, respectively).

For each individual, we annotated locations with the Human Footprint Index (HFI), an index with a global extent that combines multiple proxies of human influence: the extent of built environments, crop land, pasture land, human population density, night-time lights, railways, roads and navigable waterways (9) (see Supplementary Methods for details). The HFI ranges from 0 (natural environments: e.g., the Brazilian Pantanal) to 50 (high-density built environments: e.g., New York City).

In addition to the human footprint, we included other covariates that are known to influence mammalian movements. First, mammals generally move farther in environments with lower productivity, because individuals may need to cover a larger area to gather sufficient resources (10). To capture this effect, we annotated locations with the Normalized Difference Vegetation Index (NDVI), a well-established, satellite-derived measure of resource abundance for herbivores and carnivores alike (11). Second, an allometric scaling relationship shows that animals of greater body size usually move farther (12), and third, diet may influence movements due to differences in foraging costs and availability of resource types (13, 14). To capture these effects, we annotated the database with species averages for body size, and dietary guild (i.e., carnivore, herbivore or omnivore).

We then calculated displacements as the distance between subsequent GPS locations of each individual at nine time scales (15) ranging from one hour to ten days. For each individual at each time scale, we calculated the 0.5 and the 0.95 quantiles of displacement. The combination of different time scales and quantiles allowed us to examine the effect of the human footprint on both the median (0.5 quantile) and long-distance (0.95 quantile) movements for within-day movements (e.g., 1-hour time scale) up to longer time displacements of over one week (e.g., 10-day time scale). We used linear mixed effects models that, in addition to all covariates (i.e.,

NDVI, body mass, diet), also accounted for taxonomy and spatial autocorrelation (see Supplementary Methods for details).

We found strong negative effects of the human footprint on median and long-distance displacements of terrestrial mammals (Fig. 2a and b, Fig. 3a and Supplementary Table S3). Displacements of individuals (across species) living in areas of high human footprint (HFI = 36) were up to three times shorter than displacements of individuals living in areas of low human footprint (HFI = 0). For example, median displacements over ten days were 3.3 km (\pm SE: 1.4 km) in areas of high human footprint vs. 6.9 km (\pm SE: 1.3 km) in areas of low footprint (Fig. 2a, Table Supplementary Table S3). Likewise, the maximum displacement distances at the 10-day scale averaged 6.6 km (\pm SE: 1.4 km) in areas of high vs. 21.5 km (\pm SE: 1.4 km) in areas of low human footprint (Fig. 2a, Supplementary Table S3). The effect was significant on all temporal scales with more than eight hours between locations.

The effect was not significant at shorter time scales (Fig. 3a, 1 - 4h), suggesting that the human footprint affects ranging behavior and area use over longer time scales, rather than altering individual travel speeds (i.e., individuals may travel at the same speed if measured across short time intervals, but have more tortuous movements in areas of higher human footprint and thus remain in the same locale if displacement is measured across longer time intervals).

Reduction in movement may be due to an (1) individual-behavioral effect, where individuals alter their movements relative to the human footprint, or (2) a species-occurrence effect, where certain species that exhibit long-range movement simply do not occur in areas of high human footprint. To disentangle these two effects, we ran additional models where we separated the HFI into two components: (1) the individual-behavioral effect represented by the individual variability of HFI relative to the species mean (i.e., the individual HFI minus the species mean HFI), and (2) the species-occurrence effect as the mean HFI for each species.

Results from the two-component model indicate behavioral as well as species effects. We found a significant behavioral effect on median displacements and on long-distance displacements (0.95 quantiles) at most timescales (from eight hours to ten days) (Supplementary Fig. 2a, Supplementary Table S4). The species-occurrence effect was significant only over longer timescales (128 and 256 hour periods or 5 and 10 days, respectively) (Supplementary Fig. 2b, Supplementary Table S4). However, we note that the estimate of the species-occurrence effect is conservative because our model incorporated taxonomy as a random effect. Some variability in the data may have been accounted for by the species-level random effect rather than the species-level HFI (see Table S3).

In addition to the human footprint effect, body mass, dietary guild, and resource availability were also related to movement distances. First, as expected from allometric scaling and established relationships of body size with home range size (14) and migration distance (16), larger species travelled farther than smaller species (Fig. 3c, Supplementary Table S3 and S4). Second, we found a negative relationship between resource availability and displacement distance such that movements were on average shorter in environments with higher resources (Fig. 3b, Supplementary Table S3 and S4). These results are consistent with reports of larger home range size (17) and longer migration distance (18) in mammals living in resource-poor environments. Finally, our analyses showed that carnivores travelled on average farther per unit time than herbivores and omnivores (Supplementary Table S3 and S4). These results concur with prior understanding that carnivores have larger home range sizes (14) because they need to find mobile prey and compensate for energy conversion loss through the food web. For all of these variables, effects were significant across time scales longer than eight hours for both median and long-distance displacements.

The reduction of mammalian movements in areas of high HFI likely stems from two non-exclusive mechanisms; 1) movement barriers such as habitat change & fragmentation (19, 20); and 2) reduced movement requirements due to enhanced resources (e.g., crops, supplemental feeding and water sources (5, 21)). Studies have shown both mechanisms at work with varying responses across populations or species (see Supplementary Table S5 for examples). In some cases, they act together on single individuals or populations – for example, red deer in Slovenia have smaller home ranges due to the enhancement of resources via supplemental feeding and the disturbance and fragmentation caused by the presence of roads (22).

While these mechanisms can have differential effects on population densities (i.e., increases under supplementation (23) and decreases under fragmentation (24)) the consequences of reduced vagility affects ecosystems regardless of the underlying mechanisms and go far beyond the focal individuals themselves. Animal movements are essential for ecosystem functioning as they act as mobile links (25) and mediate key processes such as seed dispersal, food-web dynamics including herbivory and predator-prey interactions, and metapopulation- and disease dynamics (26). Single species or single site studies have shown the severe effects of reduced vagility on these processes (27, 28). The global nature of reduced vagility across mammalian species that we demonstrate here suggests consequences for ecosystem functioning worldwide. Future landscape management should include animal movements as a key conservation metric and aim towards maintaining landscape permeability. Ultimately, because of the critical role of animal movement for human-wildlife coexistence (29) and disease spread (30), effects of reduced vagility may go beyond ecosystem functioning and directly affect human well-being.

Figures

Fig. 1 Locations from the GPS tracking database and the Human Footprint Index. (A) GPS relocations of 803 individuals across 57 species plotted on the global map of the Human Footprint Index (HFI) spanning from 0 (low; yellow) to 50 (high; red). (B) Examples of the landscapes under different levels of HFI; 2 HFI (the Pantanal, Brazil), 20 HFI (Bernese Alps, Switzerland), 30 HFI (Freising, Germany), and 42 HFI (Albany, New York State, U.S.A.). (C) Species averages of 10-day long-distance displacement (0.95 quantiles of individual displacements).

Fig. 2 Mammalian displacement in relation to the Human Footprint Index. (A) Median and (B) long-distance (0.95 quantile) displacements decline with increasing Human Footprint Index at the 10-day scale ($n = 48$ species and 624 individuals). Plots include a smoothing line from a locally weighted polynomial regression. A Human Footprint Index of 0 indicates areas of low human footprint, and a value of 40 represents areas of high human footprint.

Fig. 3 Model coefficients (\pm CI) of linear mixed effects models predicting mammalian displacements using the (A) Human Footprint Index (HFI), (B) Normalized Difference Vegetation Index (NDVI), and (C) body mass. Models were run for the median (blue) and long-distance (0.95 quantiles; red) displacements of each individual calculated across different time scales. When the error bars cross the horizontal line the effect is not significant. See Supplementary Tables S3 for details.

Figures

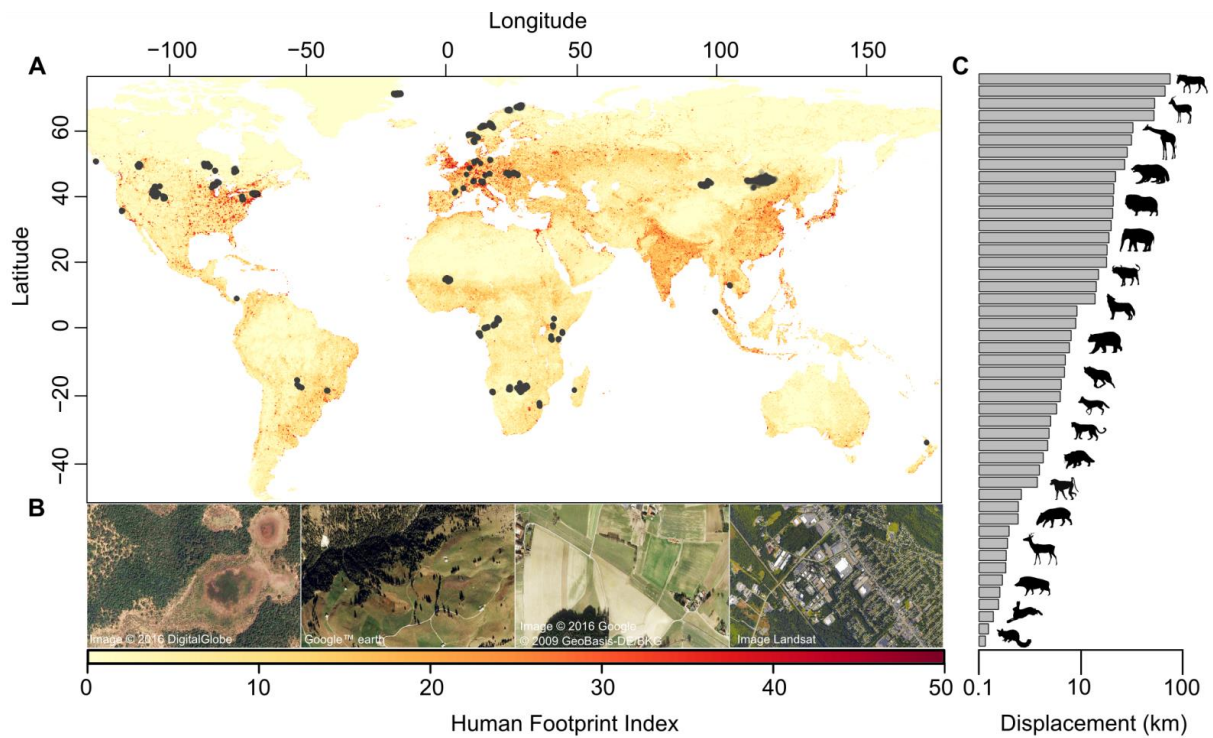


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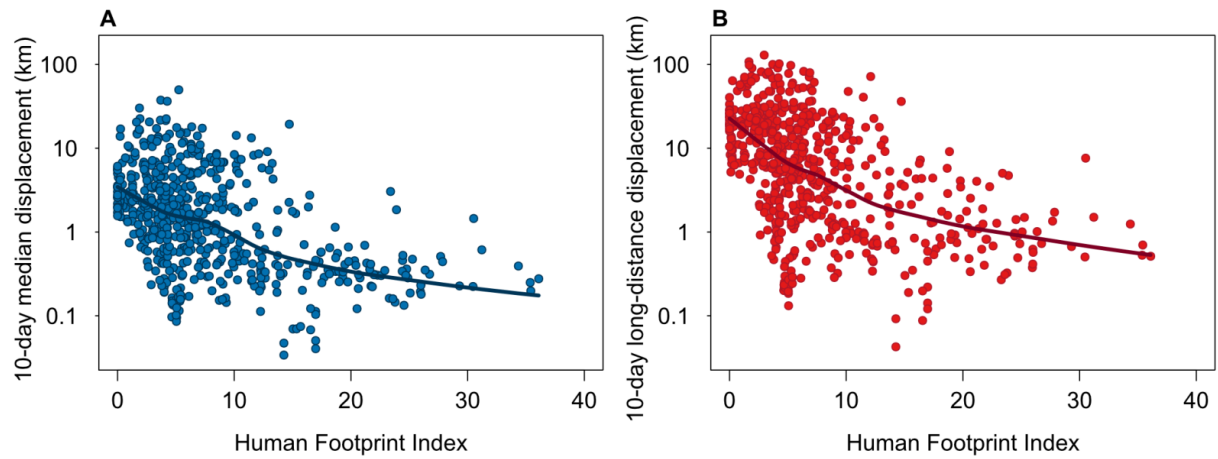


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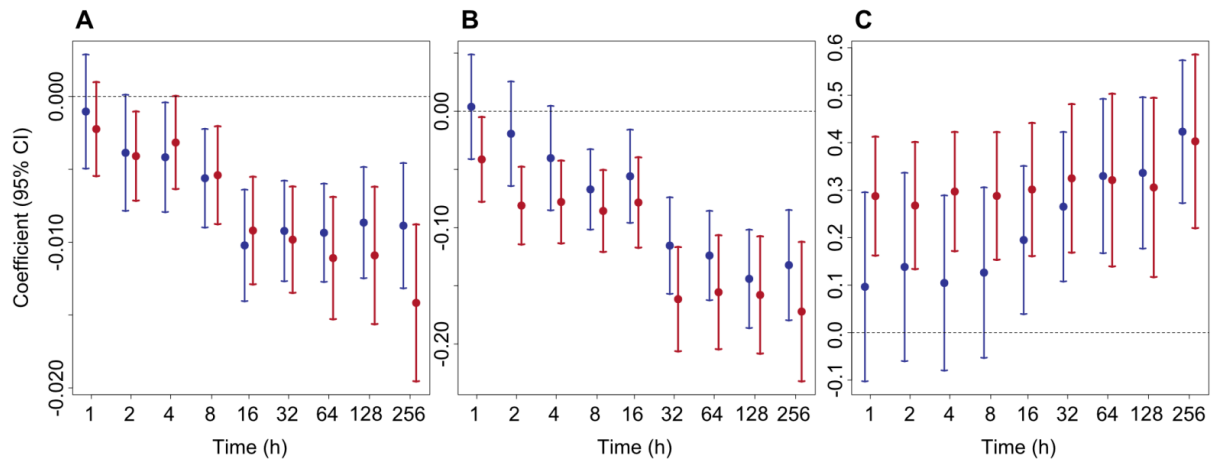


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Supplementary Materials for

Moving in the Anthropocene: Global Reductions in Terrestrial Mammalian Movements

Marlee A. Tucker, Katrin Böhning-Gaese, William F. Fagan, John M. Fryxell, Bram Van Moorter, Susan C. Alberts, Abdullahi H. Ali, Andrew M. Allen, Nina Attias, Tal Avgar, Hattie Bartlam-Brooks, Bayarbaatar Buuveibaatar, Jerrold L. Belant, Alessandra Bertassoni, Dean Beyer, Laura Bidner, Floris M. van Beest, Stephen Blake, Niels Blaum, Chloe Bracis, Danielle Brown, PJ Nico de Bruyn, Francesca Cagnacci, Justin M. Calabrese, Constança Camilo-Alves, Simon Chamailié-Jammes, Andre Chiaradia, Sarah C. Davidson, Todd Dennis, Stephen DeStefano, Duane Diefenbach, Iain Douglas-Hamilton, Julian Fennessy, Claudia Fichtel, Wolfgang Fiedler, Christina Fischer, Ilya Fischhoff, Christen H. Fleming, Adam T. Ford, Susanne A. Fritz, Benedikt Gehr, Jacob R. Goheen, Eliezer Gurarie, Mark Hebblewhite, Marco Heurich, A. J. Mark Hewison, Christian Hof, Edward Hurme, Lynne A. Isbell, René Janssen, Florian Jeltsch, Petra Kaczensky, Adam Kane, Peter Kappeler, Matthew Kauffman, Roland Kays, Duncan Kimuyu, Flavia Koch, Bart Kranstauber, Scott LaPoint, Peter Leimgruber, John D. C. Linnell, Pascual López-López, A. Catherine Markham, Jenny Mattisson, Emilia Patricia Medici, Ugo Mellone, Evelyn Merrill, Guilherme de Miranda Mourão, Ronaldo G. Morato, Nicolas Morellet, Thomas Morrison, Samuel L Díaz-Muñoz, Atle Mysterud, Dejid Nandintsetseg, Ran Nathan, Aidin Niamir, John Odden, Robert B. O'Hara, Luiz Gustavo R. Oliveira-Santos, Kirk A. Olson, Bruce D. Patterson, Rogerio Cunha de Paula, Luca Pedrotti, Björn Reineking, Martin Rimmner, Tracey L. Rogers, Christer Moe Rolandsen, Christopher S. Rosenberry, Daniel I. Rubenstein, Kamran Safi, Sonia Saïd, Nir Sapir, Hall Sawyer, Niels Martin Schmidt, Nuria Selva, Agnieszka Sergiel, Enkhtuvshin Shiilegdamba, João Paulo Silva, Navinder Singh, Erling J. Solberg, Orr Spiegel, Olav Strand, Siva Sundaresan, Wiebke Ullmann, Ulrich Voigt, Jake Wall, David Wattles, Martin Wikelski, Christopher C. Wilmers, John W. Wilson, George Wittemyer, Filip Zięba, Tomasz Zwijacz-Kozica, Thomas Mueller

Correspondence Author. Email: tucker.marlee@gmail.com;
thomas.mueller@senckenberg.de

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Materials and Methods

Displacement Data

We compiled GPS location data for 57 mammalian species, comprising 7 339 376 locations of 803 individuals from 1998 to 2015 (Fig. 1, Supplementary Table S1). The dataset included adult male and female individuals. Datasets were obtained from the online animal tracking database *Movebank* (<https://www.movebank.org/>), the Movebank Data Repository (*Equus quagga* (1, 2) and *Loxodonta africana* (3, 4)), or were contributed by co-authors directly (Table S2). For species that are inactive at night (e.g., primates sleeping overnight in trees) and where the GPS devices had been switched off to prolong battery life, we interpolated location data during the inactive phase (i.e., using the last recorded position) with the same sampling frequency as that employed for active periods to ensure an even sampling regime.

We sub-sampled the location data with inter-location intervals at a geometric time scale from one hour to ~ ten days (i.e. 1, 2, 4, 8, 16, 32, 64, 128 and 256 hours) using the “SyncMove” R package (5). We started the sub-sampling algorithm from the first location recorded for each individual. For each of the nine time scales, we calculated the geodesic distance between the subsampled locations using the Spherical Law of Cosines using 6371 km as the mean radius of the Earth (6). This allowed a systematic investigation across time scales from within day movements to more long-term movements, and standardized the sampling regime across studies and individuals. Smaller time intervals were not available for most species and longer time intervals resulted in a significant loss in sample size. Sub-sampling precision was set to the inter-location interval $\pm 4\%$ (e.g., for the 1-hour scale resulting in inter-location intervals varying between 57 and 62 minutes). We then checked the data for outliers, specifically for maximum movement speeds that were unlikely for a terrestrial land mammal to achieve over a given time period ($> 4 \text{ m s}^{-1}$), and removed them (7). We calculated two response variables for each individual: the 0.5 quantile displacement distance and the 0.95 quantile displacement distance, the former describing the median movement behavior of that individual, and the latter describing long-distance movements (Supplementary Figure S1). All values were \log_{10} transformed prior to analyses.

Covariates

We annotated each GPS location with NDVI and human footprint index (8) (HFI; Supplementary Table S2). NDVI data was extracted from MODIS Land Terra Vegetation Indices 500-m 16-day resolution (MOD13A1 V005 (9)) using the Movebank Env-DATA system (10) (environmental-data automated track annotation; <http://www.movebank.org>). We filtered the NDVI data to remove pixels with no data (-1), snow/ice (2) and clouds (3). We also included species body mass using the PanTHERIA database (11) (where individual mass information was unknown) and diet (i.e., carnivore, herbivore or omnivore) (Table S1). Body mass values were \log_{10} transformed and the NDVI values were scaled. We then calculated the mean NDVI and human footprint value for each

inter-location interval (i.e., the average value between each sequential pair of locations) and averaged these values for each individual.

Analyses

Our final database (Supplementary Fig. 1) comprised nine median and nine 0.95 quantile movement distance values for each individual (one for each temporal scale), associated with nine mean values for body mass, NDVI, and the human footprint index. We only included individuals that had tracking data for a minimum of two months (~60 days) or 50 displacements. We ran 18 linear mixed effects models, two for each time-scale, one with the 0.5 and the other with the 0.95 quantile displacement distances as the dependent variable, and body mass, NDVI, HFI, and diet as the predictor variables. We included species identity as a nested random effect to account for taxonomy (i.e., Order/Family/Genus/Species), and a Gaussian spatial autocorrelation structure (12) including the mean longitude and latitude for each individual. For each model, we checked the residuals for normality (i.e., Q-Q plots) and removed outliers (< 2% of total data points). All correlation coefficients among the predictor variables were $|r| \leq 0.55$ and all variance inflation factors (VIFs) were ≤ 2 , well below the common cut-off values of 0.7 and 4, respectively (13, 14). All model predictions and associated standard errors were calculated using the “AICcmodavg” R package (15). All analyses were performed in R version 3.2.2 (16).

Supplementary Text

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Institute for Ornithology and the Movebank Data Repository is hosted by the University of Konstanz. Roe and red deer data were obtained from eouroungulates, www.eouroungulates.org. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government. Figure 1 silhouettes by J. A. Venter, H. H. T. Prins, D. A. Balfour & R. Slotow (vectorized by T. M. Keesey) (hare and buffalo) and R. Groom (gazelle) were downloaded from www.phylopic.org are available for re-use under the Creative Commons Attribution 3.0 Unported license. Figure 1 silhouettes by S. Traver (boar, deer, tapir, wildcat, elephant, muskox, wolverine, giraffe and khulan), O. Jones (baboon), D. Orr (coyote), T. Heath (bear and wolf) and G. Prideaux (possum) were downloaded from www.phylopic.org and are available for re-use under the Public Domain Mark 1.0 license. Puma, maned wolf and lynx silhouettes by M. Tucker.

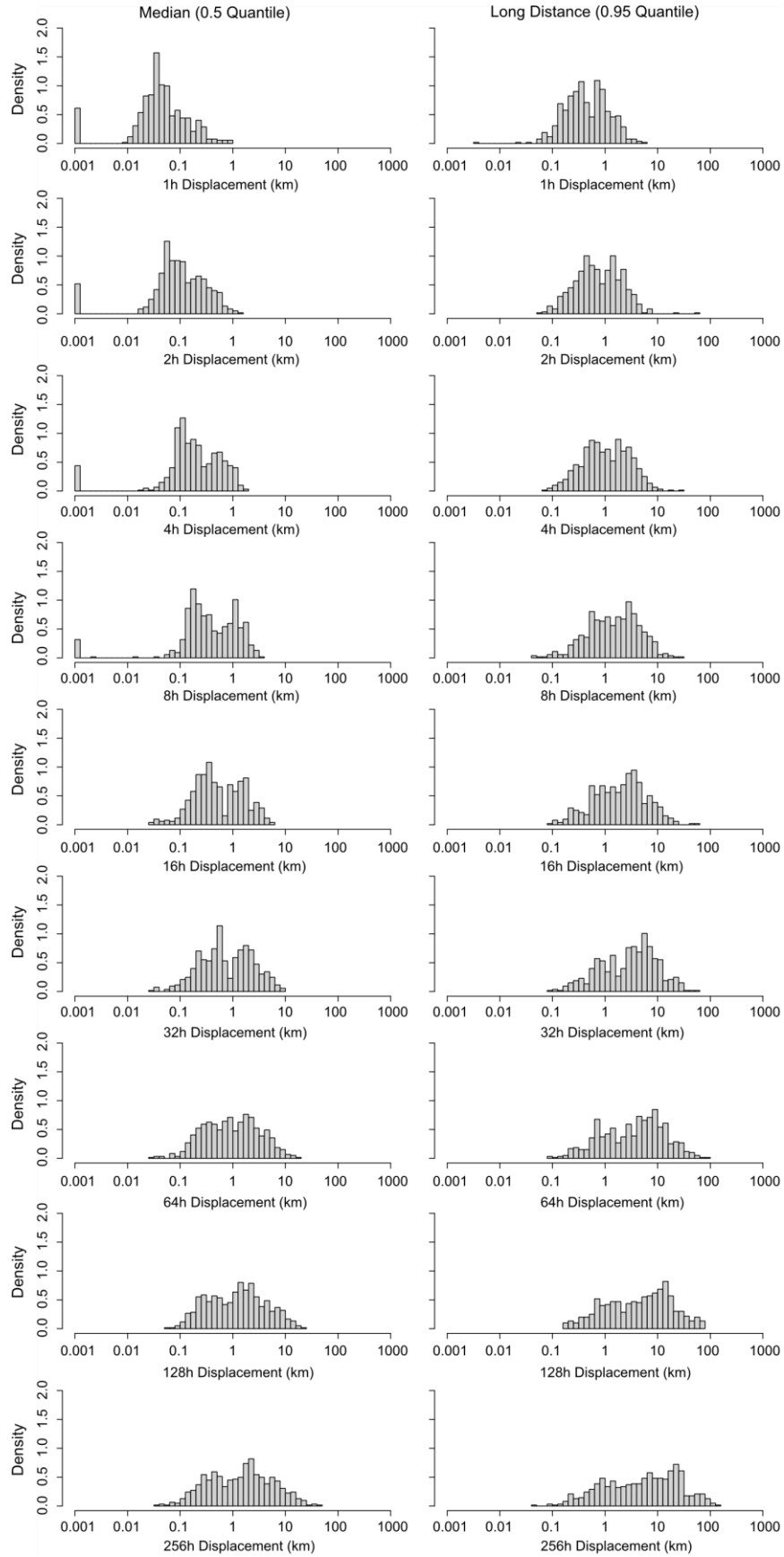


Fig. S1.

Distributions of the median and 0.95 quantiles of the individual displacements used in the analyses. The y-axis represents the density distribution of median (0.5 quantile) and long-distance (0.95 quantile) displacements of each individual.

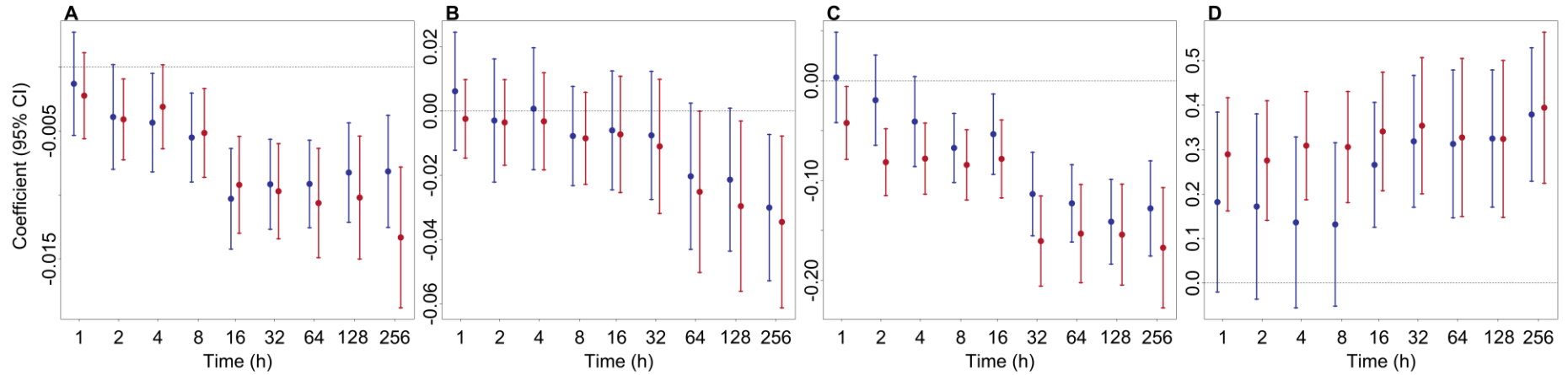


Fig. S2

Model coefficients (\pm CI) predicting mammalian displacements including (A) an individual-behavioral effect and (B) a species-occurrence effect of the Human footprint index (HFI). The individual-behavioral HFI was calculated as the individual HFI minus the species mean HFI, and the species-occurrence HFI was calculated as the species mean HFI. Other covariates of the model included (C) Normalized Difference Vegetation Index (NDVI), (D) body mass, and dietary guild (not shown). The models also included a nested random effect accounting for taxonomy, and a Gaussian spatial autocorrelation structure. Models were run for the median (i.e. -0.5 quantiles; blue) and long-distance (i.e. 0.95 quantiles; red) displacements of each individual calculated across different time scales. When the error bars cross the horizontal line (at 0) the effect is not significant. See Methods and Supplementary Tables S4 for additional details.

Table S1.

Data annotation summary

Variable	Unit	Temporal Resolution	Spatial Resolution	Source	Transformation
Normalised Difference Vegetation Index (NDVI)	Unitless	16 days	500 m	MODIS Land Terra Vegetation Indices 500-m 16-day (MOD13A1 V005)	Scaled
Human Footprint	Unitless	1993-2009 mean	1 km	Global terrestrial Human Footprint maps for 1993 and 2009 (8, 17)	Log ₋₁₀
Body Mass	Grams	Not applicable.	Not applicable.	K. E. Jones <i>et al.</i> , PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. <i>Ecology</i> . 90 , 2648 (2009).	Log ₋₁₀
Diet	Unitless, categorical	Not applicable.	Not applicable.	K. E. Jones <i>et al.</i> , PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. <i>Ecology</i> . 90 , 2648 (2009).	Not applicable.

Table S2.

Summary of species and number of individuals per species included in the analyses.

Species	No. Individuals	Data Source	Species	No. Individuals	Data Source
<i>Aepyceros melampus</i>	20	Co-author	<i>Madoqua guentheri</i>	15	Co-author
<i>Alces alces</i>	46	Co-author	<i>Martes pennanti</i>	13	Movebank
<i>Antilocapra americana</i>	25	Co-author	<i>Myrmecophaga tridactyla</i>	4	Co-author
<i>Beatragus hunteri</i>	4	Co-author	<i>Odocoileus hemionus</i>	25	Co-author
<i>Canis aureus</i>	1	Movebank	<i>Odocoileus hemionus columbianus</i>	14	Co-author
<i>Canis latrans</i>	19	Movebank	<i>Odocoileus virginianus</i>	30	Movebank
<i>Canis lupus</i>	12	Co-author & Movebank	<i>Ovibos moschatus</i>	14	Co-author
<i>Capreolus capreolus</i>	94	Eurodeer & co-author	<i>Panthera leo</i>	2	Movebank
<i>Cercocebus galeritus</i> *	1	Co-author	<i>Panthera onca</i>	4	Co-author
<i>Cerdocyon thous</i>	10	Co-author	<i>Panthera pardus</i>	4	Movebank
<i>Cervus elaphus</i>	47	Co-author, Eurodeer & Movebank	<i>Papio anubis</i>	4	Movebank
<i>Chlorocebus pygerythrus</i>	12	Movebank	<i>Papio cynocephalus</i> *	22	Co-author & Movebank
<i>Chrysocyon brachyurus</i>	12	Movebank	<i>Procapra gutturosa</i>	15	Co-author
<i>Connochaetes taurinus</i>	3	Co-author	<i>Procyon lotor</i>	9	Movebank
<i>Dasyurus novemcinctus</i>	1	Co-author	<i>Propithecus verreauxi</i> *	28	Co-author
<i>Elephas maximus</i>	2	Movebank	<i>Puma concolor</i>	6	Co-author
<i>Equus grevyi</i>	7	Movebank	<i>Rangifer tarandus</i>	14	Co-author
<i>Equus hemionus</i>	6	Co-author	<i>Saguinus geoffroyi</i> *	3	Movebank
<i>Equus quagga</i>	27	Co-author & Movebank	<i>Saiga tatarica</i>	3	Co-author
<i>Eulemur rufifrons</i>	4	Co-author	<i>Sus scrofa</i>	26	Co-author
<i>Euphractus sexcinctus</i>	7	Co-author	<i>Syncerus caffer</i>	6	Movebank
<i>Felis silvestris</i>	5	Movebank	<i>Tamandua mexicana</i>	2	Movebank
<i>Giraffa camelopardalis</i>	5	Co-author	<i>Tapirus terrestris</i>	4	Co-author
<i>Gulo gulo</i>	5	Co-author	<i>Tolypeutes matacus</i>	5	Co-author
<i>Lepus europaeus</i>	39	Movebank	<i>Trichosurus vulpecula</i> *	29	Co-author
<i>Loxodonta africana</i>	14	Co-author & Movebank	<i>Ursus americanus</i>	21	Movebank
<i>Loxodonta africana cyclotis</i>	23	Movebank	<i>Ursus arctos</i>	13	Co-author
<i>Lynx lynx</i>	6	Co-author	<i>Vulpes vulpes</i>	5	Movebank
<i>Lynx rufus</i>	6	Movebank			

* GPS devices turned off during inactive periods to save battery (e.g., primates sleeping overnight in trees) and location data was interpolated during the stationary phases (see Methods in main text).

Table S3.

Model coefficients, r-squared and sample sizes of linear mixed effects models predicting the median and 0.95 quantiles of individual displacements from 1 to 256 hour time scales. Predictor variables included body mass, NDVI, diet and the human footprint index. The model also included a nested random effect accounting for the taxonomy, and a Gaussian spatial autocorrelation structure. We calculated the marginal r^2 (variance explained by the fixed effects) and conditional r^2 (variance explained by both fixed and random factors) values for each model using the “MuMIn” R package (18). Fixed effects included mass, NDVI, the human footprint index and diet. Random effects included taxonomy. *p<0.05, **p<0.01, ***p<0.001

	1h		2h		4h		8h		16h		32h		64h		128h		256h	
	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%
Mass	0.096	0.288***	0.138	0.268***	0.105	0.297***	0.126	0.288***	0.195*	0.301***	0.265***	0.325***	0.33***	0.321***	0.336***	0.306**	0.423***	0.403***
NDVI	0.004	-0.041*	-0.019	-0.081***	-0.04	-0.078***	-0.067***	-0.086***	-0.056**	-0.078***	-0.115***	-0.161***	-0.124***	-0.155***	-0.144***	-0.158***	-0.132***	-0.172***
HumanF	-0.001	-0.002	-0.004	-0.004*	-0.004	-0.003	-0.006***	-0.005**	-0.01***	-0.009***	-0.009***	-0.01***	-0.009***	-0.011***	-0.009***	-0.011***	-0.009***	-0.014***
Diet (H)	0.225	-0.209	0.175	-0.172	-0.018	-0.363	-0.026	-0.431	-0.342	-0.497*	-0.552*	-0.598*	-0.72**	-0.527	-0.558*	-0.342	-0.638*	-0.46
Diet (O)	0.185	-0.127	0.052	-0.066	-0.006	-0.186	0.073	-0.233	-0.123	-0.248	-0.307	-0.403	-0.494	-0.445	-0.45*	-0.346	-0.492*	-0.398
r² Marginal	0.034	0.286	0.045	0.255	0.016	0.346	0.022	0.35	0.228	0.415	0.349	0.443	0.406	0.347	0.391	0.28	0.459	0.381
r² Conditional	0.922	0.865	0.932	0.895	0.958	0.887	0.977	0.901	0.875	0.885	0.898	0.898	0.906	0.87	0.871	0.846	0.866	0.835
Species	52		53		48		45		42		41		43		46		48	
Individuals	531		606		601		544		525		526		590		598		624	

Table S4.

Model coefficients, r-squared and sample sizes of linear mixed effects models predicting the median and 0.95 quantiles of individual displacements from 1 to 256 hour time scales. Predictor variables included body mass, NDVI, diet and the human footprint index, which was split into the individual-behavioral effect (Ind_HumanF: the individual HFI minus the species mean HFI) and species-occurrence effect (Sp_HumanF: the species mean HFI). The model also included a nested random effect accounting for the taxonomy, and a Gaussian spatial autocorrelation structure. We calculated the marginal r^2 (variance explained by the fixed effects) and conditional r^2 (variance explained by both fixed and random factors) values for each model using the “MuMIn” R package(18). Fixed effects included mass, NDVI, the human footprint index and diet. Random effects included taxonomy. *p<0.05, **p<0.01, ***p<0.001

	1h		2h		4h		8h		16h		32h		64h		128h		256h	
	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%	Median	95%
Mass	0.129	0.287***	0.143	0.267***	0.127***	0.292	0.116	0.268***	0.203*	0.301***	0.254**	0.301***	0.271**	0.236*	0.279**	0.218*	0.373***	0.33***
NDVI	0.003	-0.041*	-0.019	-0.08***	-0.041	-0.077***	-0.067***	-0.085***	-0.056*	-0.078***	-0.115**	-0.16***	-0.122**	-0.152*	-0.142**	-0.154*	-0.127***	-0.166***
Ind_HumanF	-0.001	-0.002	-0.004	-0.004*	-0.004*	-0.003	-0.006**	-0.005**	-0.01***	-0.009***	-0.009***	-0.01***	-0.009***	-0.011***	-0.008***	-0.01***	-0.008***	-0.013***
Sp_HumanF	0.005	-0.002	-0.003	-0.004	0.001	-0.005	-0.008	-0.01	-0.008	-0.009	-0.011	-0.015	-0.022	-0.031	-0.025	-0.036*	-0.031*	-0.038*
Diet (H)	0.206	-0.209	0.168	-0.172	-0.023	-0.36	-0.035	-0.421	-0.352	-0.497*	-0.544*	-0.571*	-0.626*	-0.46	-0.477	-0.304	-0.66**	-0.42
Diet (O)	0.169	-0.126	0.047	-0.066	-0.018	-0.185	0.068	-0.233	-0.131	-0.249	-0.301	-0.383	-0.424	-0.384	-0.381	-0.288	-0.499*	-0.356
r^2 Marginal	0.037	0.282	0.045	0.252	0.016	0.342	0.023	0.345	0.222	0.407	0.343	0.433	0.394	0.367	0.406	0.323	0.528	0.428
r^2 Conditional	0.921	0.866	0.932	0.896	0.958	0.889	0.978	0.905	0.874	0.886	0.901	0.902	0.913	0.886	0.884	0.87	0.882	0.853
Species	52		53		48		45		42		41		43		46		48	
Individuals	531		606		601		544		525		526		590		598		624	

Table S5.

Summary of the positive (+) and negative (-) effects of barriers and anthropogenic resources on individuals, populations and ecosystems using examples from the literature.

Mechanism	Impact	Level of Impact	Effect of impact	Study Organism	References
Restricted Access to Natural Areas/Barriers	Road barriers alter genetic structure between populations.	Populations	-	Moose (<i>Alces alces</i>); desert bighorn sheep (<i>Ovis canadensis nelsoni</i>)	Wilson <i>et al.</i> (19); Epps <i>et al.</i> (20)
	Altered animal abundance.	Populations	-/+	White-tailed antelope squirrel (<i>Ammospermophilus leucurus</i>), black-tailed prairie dog (<i>Cynomys ludovicianus</i>), Merriam's kangaroo rat (<i>Dipodomys merriami</i>), kangaroo rat (<i>Dipodomys microps</i>), prairie vole (<i>Microtus ochrogaster</i>), California vole (<i>Microtus californicus</i>), house mouse (<i>Mus musculus</i>), woodrat (<i>Notoma lepida</i>), golden mouse (<i>Ochrotomys nuttalli</i>), long-tailed pocket mouse (<i>Perognathus formosus</i>), white-footed mouse (<i>Peromyscus boylii</i>), white-footed mouse (<i>Peromyscus leucopus</i>), deer mouse (<i>Peromyscus maniculatus</i>), rat (<i>Rattus rattus</i>), eastern chipmunk (<i>Tamias striatus</i>), chacoan peccary (<i>Catagonus wagneri</i>), hedgehog (<i>Erinaceus europaeus</i>), brown hare (<i>Lepus europaeus</i>), American marten (<i>Martes americana</i>), badger (<i>Meles meles</i>), koala (<i>Phascolarctos cinereus</i>), white-lipped peccary (<i>Tayassu pecari</i>), collared peccary (<i>Tayassu tajacu</i>), red fox (<i>Vulpes vulpes</i>), Impala (<i>Aepyceros</i>)	Fahrig <i>et al.</i> (21)

				<i>melampus</i>), moose (<i>Alces alces</i>), wolf (<i>Canis lupus</i>), eastern timber wolf (<i>Canis lupus lycaon</i>), black-backed jackal (<i>Canis mesomelas</i>), roe deer (<i>Capreolus capreolus</i>), elk (<i>Cervus canadensis</i>), wildebeest (<i>Connochaetes taurinus</i>), zebra (<i>Equus quagga</i>), giraffe (<i>Giraffa camelopardalis</i>), African elephant (<i>Loxodonta africana</i>), bobcat (<i>Lynx rufus</i>), Eurasian lynx (<i>Lynx lynx</i>), Iberian lynx (<i>Lynx pardinus</i>), mule deer (<i>Odocoileus hemionus</i>), Amur tiger (<i>Panthera tigris altaica</i>), warthog (<i>Phacochoerus africanus</i>), cougar (<i>Puma concolor</i>), woodland caribou (<i>Rangifer tarandus caribou</i>), bohor reedbuck (<i>Redunca redunca</i>), boar (<i>Sus scrofa</i>), eland (<i>Taurotragus oryx</i>), brown bear (<i>Ursus arctos</i>) and grizzly bear (<i>Ursus arctos horribilis</i>).	
	Decreased immigration and colonization success due to barriers.	Populations	-	Animal simulation	Fahrig (22)
	Reproduction, body mass and mobility impact susceptibility to roads.	Individual	-/+	Woodland caribou (<i>Rangifer tarandus</i>), white-footed mouse (<i>Peromyscus leucopus</i>), eastern chipmunk (<i>Tamias striatus</i>), hedgehog (<i>Erinaceus europaeus</i>), bobcat (<i>Lynx rufus</i>), grey wolf (<i>Canis lupus</i>), cougar (<i>Puma concolor</i>), black bear (<i>Ursus americanus</i>), elk (<i>Cervus elaphus</i>), moose (<i>Alces alces</i>) and grizzly bear (<i>Ursus arctos</i>).	Rytwinski <i>et al.</i> (23)
	Dirt tracks/firebreaks can increase seed dispersal.	Ecosystem	+	Wild boar (<i>Sus scrofa</i>), red deer (<i>Cervus elaphus</i>), fallow deer (<i>Dama dama</i>), red fox (<i>Vulpes vulpes</i>), Eurasian badger (<i>Meles meles</i>) and	Suarez-Esteban <i>et al.</i> (24)

				European hare (<i>Lepus europaeus</i>).	
	Fragmentation and altered community composition.	Individuals and populations	-	Mammal simulations	Buchmann <i>et al.</i> (25)
	Tortuosity increases near roads and trails.	Individuals	-	Wolf (<i>Canis lupus</i>)	Whittington <i>et al.</i> (26)
	Small home range and increased overlap near hard boundaries (e.g., roads) and altered genetic composition.	Individuals and populations	-	Coyote (<i>Canis latrans</i>) and bobcats (<i>Lynx rufus</i>).	Riley <i>et al.</i> (27)
	Reduced population densities near infrastructure.	Populations	-	Moose (<i>Alces alces</i>), coyote (<i>Canis latrans</i>), red fox (<i>Vulpes vulpes</i>), duiker (<i>Cephalophus</i> sp), elk (<i>Cervus canadensis</i>), blue wildebeest (<i>Connochaetes taurinus</i>), Emin's pouched rat (<i>Cricetomys emini</i>), link rat (<i>Deomys ferrugineus</i>), desert kangaroo rat (<i>Dipodomys deserti</i>), plains zebra (<i>Equus quagga</i>), red-cheeked rope squirrel (<i>Funisciurus leucogenys</i>), shining thicket rat (<i>Grammomys rutilans</i>), African dormice (<i>Graphiurus</i> sp), African smoky mouse (<i>Heimyscus fumosus</i>), Peters' striped mouse (<i>Hybomys univittatus</i>), beaded wood mouse (<i>Hylomyscus aeta</i>), Allen's wood mouse (<i>Hylomyscus allenii</i>), European hare (<i>Lepus europaeus</i>), fire-bellied brush-furred rat (<i>Lophuromys nudicaudus</i>), African elephant (<i>Loxodonta africana</i>), forest elephant (<i>Loxodonta africana cyclotis</i>), bobcat (<i>Lynx rufus</i>), fawn-footed mosaic-tailed rat (<i>Melomys cervinipes</i>), mule deer (<i>Odocoileus hemionus</i>), white-tailed deer (<i>Odocoileus virginianus</i>), Tullberg's soft-furred mouse (<i>Praomys</i>	Benitez-Lopez <i>et al.</i> (28)

				<i>tullbergi</i>), reindeer (<i>Rangifer tarandus</i>), rat (<i>Rattus</i> spp), round-tailed ground squirrel (<i>Spermophilus tereticaudus</i>), target rat (<i>Stochomys longicaudatus</i>), eland (<i>Taurotragus</i> spp), bohor reedbuck (<i>Redunca redunca</i>), giant white-tailed rat (<i>Uromys caudimaculatus</i>), brown bear (<i>Ursus arctos</i>) and black-backed jackal (<i>Canis mesomelas</i>).	
	Reduced population densities near infrastructure and restricted movements caused by infrastructure.	Populations	-	Forest elephants (<i>Loxodonta africana cyclotis</i>).	Blake <i>et al.</i> (29)
	Reduced movements due to human settlements/roads and reduced flow of females between populations.	Individuals and populations	-	Grizzly bears (<i>Ursus arctos</i>).	Proctor <i>et al.</i> (30)
Restricted Access AND Increased Resources	Movements tied to artificial water sources and increased recursive movements due to fences, resulting in increased pressure on local resources.	Individuals, populations and ecosystems	-	African elephant (<i>Loxodonta africana</i>).	Loarie <i>et al.</i> (31)
	Smaller home ranges due to supplemental feeding and road barriers.	Individuals and populations	-	Red deer (<i>Cervus elaphus</i>)	Jerina <i>et al.</i> (32)
	Urban resources as an ecological trap: urban sink populations and urban islands impact population genetic structure/flow and increase in conflict with humans due to expanding population numbers.	Individuals and populations	-	Wild boar (<i>Sus scrofa</i>)	Stillfried <i>et al.</i> (33)
	Increased productivity/reproduction, altered migration timing and increased grazing pressure at winter sites due to supplemental feeding, and population declines due to habitat loss.	Individual, population and ecosystem	-/+	Mule deer (<i>Odocoileus hemionus</i>)	DeVos <i>et al.</i> (34); Sandoval <i>et al.</i> (35); Peterson <i>et al.</i> (36) ; Bishop <i>et al.</i> (37).

	Landscape elements (e.g., fruit trees) act as food supplements, allowing populations to persist in fragmented landscapes.	Individuals and populations.	+	Howler monkeys (<i>Alouatta palliata mexicana</i>)	Asensio <i>et al.</i> (38)
Increased Resources (Anthropogenic)	Crop damage leading to human-wildlife conflict.	Individuals and populations	-	Wild boars (<i>Sus scrofa</i>); Red deer (<i>Cervus elaphus</i>).	Honda <i>et al.</i> (39); Barrios-Garcia <i>et al.</i> (40); Bleier <i>et al.</i> (41)
	Increase in parasite load and diseases.	Individual and population	-	Elk (<i>Cervus canadensis</i>); white-tailed deer (<i>Odocoileus virginianus</i>).	Hines <i>et al.</i> (42); Miller <i>et al.</i> (43); Sorensen <i>et al.</i> (44)
	Increase group size.	Population	+	Arctic fox (<i>Vulpes lagopus</i>).	Elmhagen <i>et al.</i> (45)
	Increased survival rate, increased reproductive rate, improved winter condition, increased hunting, increased population growth rate and reduced density dependence, changed spatial genetic structure, reduced natural selection, increased aggression, increased stress, increased local browsing or grazing, changed plant species composition, invasion of non-native weed species, increased parasitism due to spatial aggregation and increased contact rates and reduced parasitism due to improved body condition.	Individual, population and ecosystem	-/+	European bison (<i>Bison bonasus</i>), wild boar (<i>Sus scrofa</i>), white-tailed deer (<i>Odocoileus virginianus</i>), elk (<i>Cervus canadensis</i>) and moose (<i>Alces alces</i>).	Milner <i>et al.</i> (46)
	Disruption of movement patterns, circadian rhythm, denning behavior, increased individual interactions, increase population size, culling, increase in diseases, human-animal conflict, alter natural foraging and trophic cascades.	Individual, population and ecosystem	-/+	Brown bears (<i>Ursus arctos</i>).	Penteriani <i>et al.</i> (47)
	Consumption of valuable tree species, altered social structure, space	Individual, population and	-/+	European bison (<i>Bison bonasus</i>); moose (<i>Alces alces</i>).	Kowalczyk <i>et al.</i> (48); Mathisen <i>et</i>

use and parasites.	ecosystem			<i>al. (49)</i>
Sustain populations in resource poor areas and trophic cascades.	Population and ecosystem	-/+	Dingo (<i>Canis lupus dingo</i>).	Newsome <i>et al.</i> (50, 51)
Trophic cascades.	Ecosystem	-	African wild dog (<i>Lycaon pictus</i>), yellow baboon (<i>Papio cynocephalus</i>), black-backed jackal (<i>Canis mesomelas</i>), bobcat (<i>Lynx rufus</i>), chilla fox (<i>Pseudalopex griseus</i>), coyote (<i>Canis latrans</i>), culpeo fox (<i>Pseudalopex culpaeus</i>), dhole (<i>Cuon alpinus</i>), common genet (<i>Genetta genetta</i>), Geoffroy's cat (<i>Oncifelis geoffroyii</i>), golden jackal (<i>Canis aureus</i>), Indian fox (<i>Vulpes bengalensis</i>), pampas fox (<i>Pseudalopex gymnocercus</i>), red fox (<i>Vulpes vulpes</i>) and San Joaquin kit fox (<i>Vulpes macrotis mutica</i>), Arabian wolf (<i>Canis lupus arabs</i>), black bear (<i>Ursus americanus</i>), brown bear (<i>Ursus arctos</i>), cheetah (<i>Acinonyx jubatus</i>), dingo (<i>Canis dingo</i>), Ethiopian wolf (<i>Canis simensis</i>), Eurasian lynx (<i>Lynx lynx</i>), grey wolf (<i>Canis lupus</i>), Mexican grey wolf (<i>Canis lupus baileyi</i>), Iberian lynx (<i>Lynx pardinus</i>), Iberian wolf (<i>Canis lupus signatus</i>), jaguar (<i>Panthera onca</i>), leopard (<i>Panthera pardus</i>), lion (<i>Panthera leo</i>), polar bear (<i>Ursus maritimus</i>), puma (<i>Puma concolor</i>), snow leopard (<i>Panthera uncia</i>), spotted hyena (<i>Crocuta crocuta</i>), tiger (<i>Panthera tigris</i>); white-tailed deer (<i>Odocoileus virginianus</i>); moose (<i>Alces alces</i>).	Newsome <i>et al.</i> (52); Cooper <i>et al.</i> (53); Gundersen <i>et al.</i> (54)

Increase in stress hormones.	Individual	-	Asiatic black bears (<i>Ursus thibetanus</i>).	Malcolm <i>et al.</i> (55)
Animal-human conflict: death and monetary costs.	Population	-	Brown bear (<i>Ursus arctos</i>).	Kavčič <i>et al.</i> (56)
Reduced natural selection effects on juveniles.	Individual and population	+	Red deer (<i>Cervus elaphus</i>).	Schmidt <i>et al.</i> (57)
Reduced and stable home range size due to resources.	Individual	+	Racoon (<i>Procyon lotor</i>) ; Roe deer (<i>Capreolus capreolus</i>) ; Red deer (<i>Cervus elaphus</i>); Iberian lynx (<i>Lynx pardinus</i>).	Prange <i>et al.</i> (58); Ossi <i>et al.</i> (59); Lopez-Bao <i>et al.</i> (60)
Reduce migration distance and time spent at summer grounds (less quality forage).	Individual	-	Elk (<i>Cervus canadensis</i>).	Jones <i>et al.</i> (61)
Smaller home range size, covered more distance, nocturnal activity and increase movement speeds.	Individual	+	Wild boar (<i>Sus scrofa</i>).	Podgorski <i>et al.</i> (62)
Anthropogenic food resources reduce home range size and increases home range overlap, with implications for rabies transmission between individuals.	Individual and populations	-	Indian mongoose (<i>Herpestes javanicus</i>).	Quinn <i>et al.</i> (63)
Food provisions impact movement behaviors, amplify pathogen invasion due to increased host aggregation and tolerance, but also reduces transmission if provisioned food decreases dietary exposure to parasites.	Individuals and populations	-/+	Elk (<i>Cervus canadensis</i>), long-tail macaque (<i>Macaca fascicularis</i>) , red fox (<i>Vulpes vulpes</i>), white-tailed deer (<i>Odocoileus virginianus</i>), common vampire bat (<i>Desmodus rotundus</i>) and flying fox (<i>Pteropus giganteus</i>).	Becker <i>et al.</i> (64)
Anthropogenic resources reduce home range size and increases livestock kills by wildlife.	Individuals	-	Spotted hyena (<i>Crocuta crocuta</i>).	Kolowski <i>et al.</i> (65)
Anthropogenic food reduced core home range size and increases population size.	Individuals and populations	+	Banded mongoose (<i>Mungos mungo</i>).	Gilchrist <i>et al.</i> (66)

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